Movement and Distribution of *Pleocoma* Larvae in Western Oregon Coniferous Forest Soils (Coleoptera: Scarabaeidae)[1]

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Abstract.—The movement and spatial and vertical distribution of *Pleocoma* larvae were studied in coniferous forests of western Oregon, incidental to a study of larval feeding habits. Larvae are able to burrow, using their mandibles, through hard and compact forest soil at rates up to 11 cm per day. With the exception of first stage larvae and larvae preparing to moult or pupate in early fall, most larvae actively burrow throughout the year. Larvae do not appear to travel for any length of time in any particular direction. Larval populations in forested areas in western Oregon are usually localized. More than 60 sample holes (1 m^2 and no less than 75 cm in depth) were dug searching for larvae. More than one-third produced no larvae, and populations in the others ranged from 1 to 56. Larvae were found at depths from 10 to 110 cm. Vertical distribution and, to a lesser extent, spatial distribution of larvae appear to be influenced by a combination of factors, principally soil moisture, soil temperature, and the presence or absence of a silicate clay layer. This silicate clay hardpan directly affects the distribution of smaller coniferous roots—the principal source of food for *Pleocoma* larvae.

I studied the feeding habits of *Pleocoma* larvae in some old-growth coniferous forests in western Oregon in the early 1960's (Fellin, 1975). The study began shortly after Stein (1963) confirmed that *Pleocoma* larvae feed on the roots of forest trees. Five species of *Pleocoma* were studied: *P. dubitabilis dubitabilis* Davis[2], *P. carinata* Linsley, and *P. simi* Davis primarily, and to a lesser extent *P. minor* Linsley and *P. crinita* Linsley.

Incidental to that study, other studies and observations were made on the biology, ecology, behavior, and distribution of *Pleocoma* spp. Many new localities were recorded and described. Based on these and other locality descriptions, the geographic distribution of all species of *Pleocoma* in Oregon was summarized and the habitats for *P. simi* and *P. carinata* were described (Fellin and Ritcher, 1967). Observations also were made on trapping male *Pleocoma* with female-baited traps

[2] According to Hovore (pers. comm.) the variety *dubitabilis* Davis was described in 1934 as a new variety of *Pleocoma staff* Schaufuss. Later, it was considered by Linsley to be a distinct species but inadvertently misspelled as *P. dubitalis*. This error of misspelling has persisted since that time.
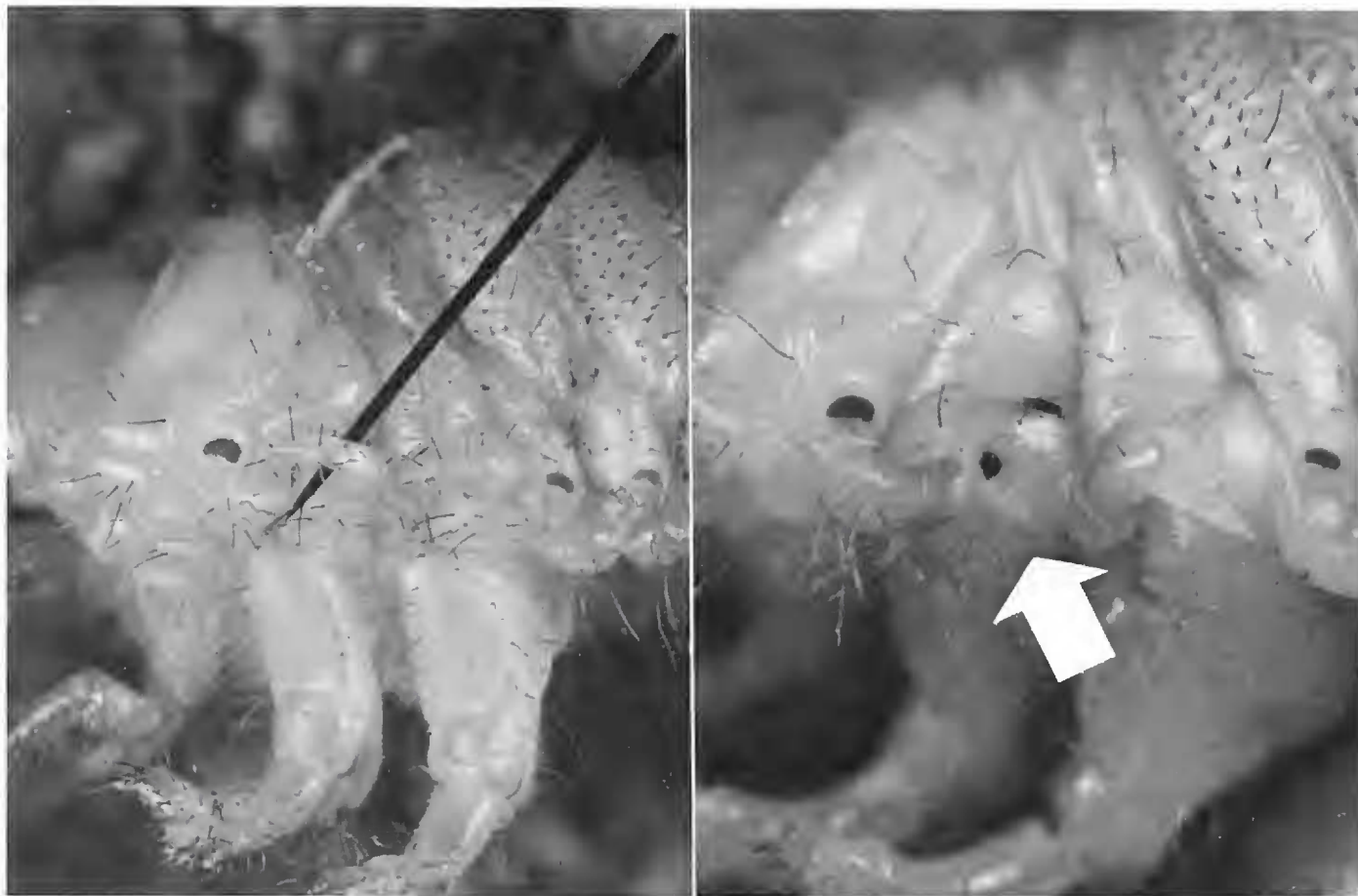
Figure 1. Technique used to mark *Pleocoma* larvae. (Left) Thoracic area of seventh instar *P. dubitabilis* showing minuten nadeln thrust through fleshy lobes at base of meso thoracic leg (15×). (Right) Thoracic area of seventh instar *P. dubitabilis* showing two black spots (arrow) caused by darkening of haemolymph where lobes were punctured by minuten nadeln (25×).

(Fellin, 1968). Observations on egg and larval biology and the flight characteristics of adults were presented elsewhere (Fellin, 1981). This paper presents results from studies of movement and spatial and vertical distribution of larvae.

MOVEMENT OF LARVAE

The movement of *P. dubitabilis* larvae in the soil was studied at a site in McDonald Forest, 8 km north of Corvallis from 1 May to 31 October 1961. I collected larvae at the study area and brought them to the laboratory for measurement and marking for later identification.

Each larva was pierced in one of its many fleshy areas, particularly along the meso-ventral line of the thorax or abdomen, with a minuten nadeln (Fig. 1A). Darkening of the haemolymph upon exposure to air left an obvious mark (Fig. 1B), and by piercing larvae on different segments or in different areas of the same segment, numerous marking combinations were achieved. I noticed no ill effects on the larvae as long as the puncture was made as far as possible out on the lobes.

Marked larvae were returned to the study area and placed in small niches in the side of a sample hole that had not been refilled with soil. The niches were then covered with a salve tin lid (Fig. 2A). After a week, lids were removed and the soil dug away until the larvae were recovered and identified (Fig. 2B).

Because it was impossible to follow larval burrows through the soil, I used an arbitrary method to determine how far larvae traveled. Vertical and lateral measurements were taken between the point at which a larva was released and the point of recovery. From these measurements I computed two distances: (1) the distance a larva would have traveled had it gone straight into the soil and then

Figure 2. Technique used in studying movement of larvae in the soil (Left) A larva is placed in a small niche provided for it in the side of an old sample hole, and the niche is covered with a salve tin lid. (Right) Searching for *Pleocoma* larvae that had been marked and placed on the side of the sample hole 1 week prior.

at a right angle downward, upward, or to the right or left (the two perpendicular sides of a right triangle), and (2) the distance traveled had it gone a direct route from the point of release to the point of recovery (the hypotenuse of a right triangle). The average of these two distances was used to estimate the distance traveled during the week, then an average rate of movement per day was calculated. Because *Pleocoma* larvae often follow winding paths through the soil, the calculated average rate of movement is probably conservative.

Burrow Construction and Method of Movement

Larvae move through the ground by biting away soil in front of them with their mandibles and depositing it to their rear as they move. Each bite of soil is momentarily held beneath the thorax by the thoracic legs. After a few bites, the larva—holding the soil by its legs, mandibles, and maxillae—turns and deposits this soil in the rear of the burrow. Here, presumably with the aid of secretions from the mouth, it is cemented against the back wall, filling the burrow behind.

Cells removed intact from the soil reveal on their edges an interesting pattern of marks made by the larval mandibles. The photographs in Figure 3 illustrate this and establish that larvae move through the soil by use of the mandibles and not by burrowing with the thoracic legs.

Larval movement through the soil depends mainly on three-point body contact. By manipulating the dorsum of the abdomen, the anal area and the thoracic legs, larvae are able to move through an open burrow fairly rapidly by pressing these three points against the walls of the burrow. *Pleocoma* larvae are well adapted for this type of movement; they possess many spine-like setae dorsally on most abdominal segments and on the caudal segments where contact is made with the soil. Necessity of three-point contact is shown by the helplessness of larvae trying to move on a flat surface.
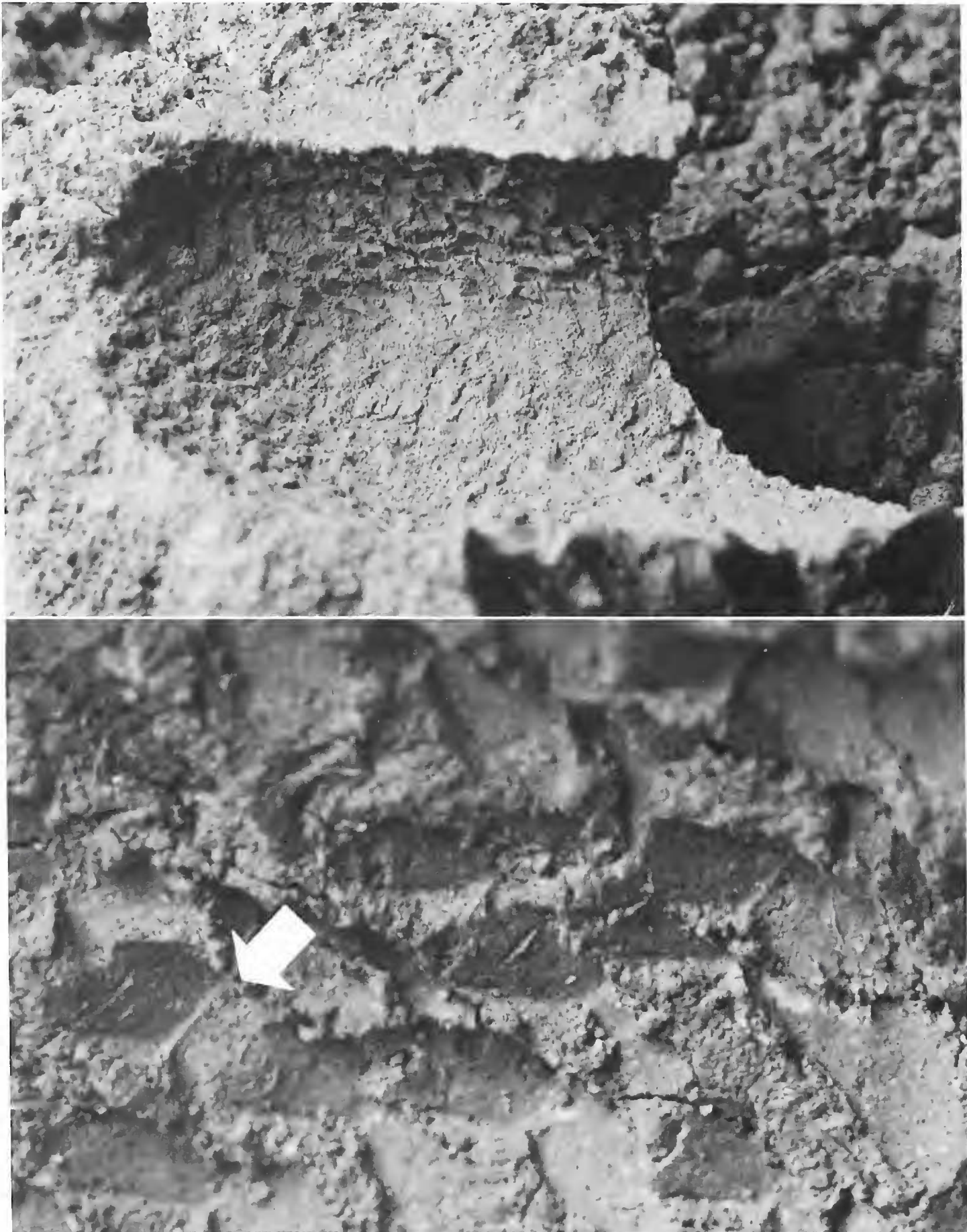
Figure 3.   Cell showing pattern made by mandibles as larvae moved through the soil. (Top) Portion of a *P. simi* cell halved lengthwise to show the mandible pattern on cell wall (2.5×). (Bottom) Closeup of individual mandible marks in the cell. Arrow points to a narrow ridge of soil formed at the point where each mandible of a pair come together (10×).

While moving through the soil, larvae maintain some distance of open burrow behind them, the length of which often varies with depth, direction, size of larva, or time of year. Fifth instar *Pleocoma* have been found with as much as 10 cm of open burrow behind them.

Table 1. Average rate of movement of *P. dubitabilis* larvae through hard and compact forest soil between early May and late October 1961.[1]

Approximate instar	No. of larvae	Average rate of movement (cm per day)
2	9	0.8
3	6	3.8
4	2	0.7
5	2	8.7
6	3	1.7
7	3	4.9
8	4	4.6
8-older	8	2.9

[1] Data are not included for larvae preparing for or recovering from a moult.

Rate of Movement

Larvae are able to move through the hard and compact forest soil at speeds varying from a little less than 1 cm per day to nearly 9 cm per day (Table 1).

Of the individual larvae observed, a fifth instar traveled the fastest, covering about 11 cm per day between 27 April and 18 May. Also, a seventh and an eighth instar burrowed 8.5 and 7.5 cm per day, respectively, during June.

Time of Year of Movement

First instars and young second instars were often collected in groups at or near the site of oviposition, indicating these small larvae do not move far. First stage larvae do not leave the egg niche moulting therein to second instars in early October. Second stage larvae have been found in egg niches in mid-November; evidently they do not begin to travel from the oviposition site until after that.

Most larvae actively burrow from early May to late October when larval movement was most intensively studied. Periodic observations from early November to late April indicate that most larvae are active during this period as well. However, between early August and late October, especially during September, there is a general period of inactivity when larvae are moulting or pupating.

The number of days that larvae ceased burrowing during the moulting period varied considerably between individuals. Some larvae slowed little in their movements prior to moulting, while others ceased movements entirely for as many as 21 days prior to the moult. Following the moult, some larvae began burrowing almost immediately and others remained motionless for as many as 24 days before they traveled again.

Direction of Movement

The inability to follow larval burrows through the soil made it difficult to determine exactly which direction the larvae moved. Of the 46 larvae studied, 31 traveled predominantly downward, two traveled down and then up, and one larva went up first and then down. Six larvae traveled horizontally, and the direction that another six traveled is not known.

It appears that *Pleocoma* larvae generally do not travel for any length of time in any particular direction. Open burrows behind larvae indicate that in the relatively short distance of 5 to 10 cm, they may have traveled in several directions.

Figure 4.   A typical larval sample collecting hole, 1 m² and about 120 cm deep.

For example, one medium-sized *P. simi* larva was found with 10 cm of open burrow behind it, and in this distance had traveled upward, turned a bit, leveled off, and turned twice more on a generally flat plane. Other Scarabaeidae larvae also change direction of movement, often doubling back in the direction from which they had burrowed (Hallock, 1935; Hawley, 1934).

There is no evidence that *Pleocoma* larvae migrate, in the sense of a continued or prolonged movement in a direction and at a rate over which they have control and resulting in a temporary or permanent change of habitat (Schneider, 1962; Williams, 1957). Movement of *Pleocoma* larvae beneath the ground can probably be characterized in terms of dispersal, defined by Schneider (1962) as a lengthening of the average distance between neighboring individuals. The abundance and distribution of the smaller coniferous roots, their principal diet in the forest environment (Fellin, 1975), no doubt also influences the movement of *Pleocoma* larvae.

DENSITY OF LARVAE IN THE SOIL

Because the primary objective of this study was to determine the feeding habits of *Pleocoma* larvae in the coniferous forest environment, the goal in collecting was to gather as many larvae as possible. Consequently, the number and location of sampling holes was purposely, and not randomly, selected.

Table 2. Spatial distribution of *P. dubitabilis* larvae in coniferous forest soil at McDonald Forest during 1961.

Date	Depth of hole (cm)	Larvae/m^2
28 January	120	21
25 February	94	[1]22
31 March	94	[2]35
28 April	75	0
29 April	90	21
29 May	130	21
28 June	120	11
28 July	120	18
15 August	100	2
13 September	124	11
21 October	110	14
21 November	105	14
22 December	105	20

[1] Unavoidable circumstances prevented the sampler from completing this hole. Had further digging been possible more larvae may have been collected.

[2] Fifteen of these 35 larvae were young second instars congregated in the same general area and probably all from the egg complement of a single female.

Sites at which sample holes were dug and larvae collected were restricted to known larval habitats or where adult males had been taken in flight. The sample hole was 1 m^2 and dug at least 75 cm deep (Fig. 4). Any hole dug 75 cm deep without larvae being found was abandoned. When larvae were found, the sample hole was dug as least 15 cm deeper than where the deepest larva was found. The depth at which larvae were collected was measured to the nearest 2 cm and depths later grouped into 10 cm classes. Other investigators have also used some of these procedures for collecting Scarab larvae—particularly determining depth of sample holes (Ellertson, 1958; Hartzell and McKenna, 1939; Shorey and Gyrisco, 1960; Travis, 1939).

Spatial Distribution of Larvae

I made 13 collections of *P. dubitabilis* larvae at the McDonald Forest study site in 1961. Larval population densities averaged 16 larvae per m^2 and ranged from 0 to 35 in sample holes varying from 75 to 130 cm in depth (Table 2).

Between May 1960 and October 1961, I made 17 collections of *P. carinata* larvae at three sites in southwestern Oregon. Larval abundance varied from 0 to 15 per m^2 in sample holes ranging from 75 to 105 cm deep (Table 3). Six of the 17 sample holes, or about 35%, produced no larvae.

Thirty-one sample holes were dug searching for *P. simi* larvae at eight sites in southwestern Oregon between May 1960 and December 1961. Fifteen of the 31 holes produced no larvae and five yielded only one larva. The two most dense populations of 34 and 56 larvae per m^2 were collected at the same site (#19) in May and March 1961, respectively (Table 4).

Four collections each of *P. crinita* and *P. minor* were made in forested areas adjacent to Hood River Valley orchards, averaging, respectively, 2 and 5 larvae per m^2.

Table 3. Spatial distribution of *P. carinata* larvae in coniferous forest soil at three forested sites in southwestern Oregon in 1960 and 1961.

Date	Site[1]	Depth of hole (cm)	Larvae/m²
2 January 1961	3	90	0
3 January 1961	3	90	0
3 January 1961	3	105	5
28 March 1961	8	90	6
10 May 1961	3	75	0
10 May 1961	3	90	2
11 May 1961	3	60	0
11 May 1961	3	105	1
12 May 1961	2	80	2
21 May 1960	2	60	0
21 May 1960	2	75	15
18 July 1961	2	90	3
19 July 1961	2	75	3
2 September 1960	2	75	3
2 September 1960	2	75	8
27 October 1961	8	75	1
27 October 1961	8	60	0

[1] The location of each site is as follows:

	Elevation
Site #2—32 km east of Medford, Jackson Co.	762–822 m
Site #3—21 km east of Butte Falls, Jackson Co.	—
Site #8—23 km northeast of Idleyld Park, Douglas Co.	700–762 m

Tables 3 and 4 show that larval populations of *P. carinata* and *P. simi* in forested areas in southwestern Oregon are very localized. Had I dug sample holes at random rather than in areas where larvae were known to occur or where adults had been collected, the densities shown in the two tables would undoubtedly have been even less.

The relative larval densities for the five species in coniferous forest soil are compared to the larval densities for three species in some orchard soils (Table 5). Larval populations in the Hood River apple orchards are quite high. Though larval populations vary widely between and within orchards, with islands of high *Pleocoma* density surrounded by areas where no larvae can be found, Zwick et al. (1970) collected 4312 *P. crinita* larvae in the soil under one mature "Newton" apple tree. One can easily see why larvae of *P. minor* and *P. crinita* are a serious economic problem in these orchards.

Vertical Distribution of Larvae

Pleocoma dubitabilis larvae were collected at the McDonald Forest study site in August and November 1960 and once each month during 1961. The vertical distribution of these larvae (Fig. 5) indicate several points of biological significance: (1) From May to September larvae were generally absent from the upper 40 cm of soil, and only five larvae, all of a size large enough to pupate, were found at depths shallower than 40 cm. (2) Larvae were generally deeper in the soil in July than in any other summer month; with the exception of two larvae, none were found shallower than 60 cm in July. (3) Between October and April, excluding

Table 4.   Spatial distribution of *P. simi* larvae in coniferous forest soil at eight forested sites[1] in southwestern Oregon in 1960 and 1961.

Date	Site[2]	Depth of hole (cm)	Larvae/m^2
7 January 1961	14	75	12
22 March 1961	19	130	[2]56
22 March 1961	19	90	0
19 May 1960	10	60	0
19 May 1960	10	60	1
20 May 1960	55	75	0
20 May 1960	55	75	0
22 May 1961	27	75	0
22 May 1961	27	90	0
22 May 1961	27	75	0
26 May 1961	19	120	34
9 June 1960	14	60	1
9 June 1960	14	60	0
9 June 1960	14	60	0
9 June 1960	14	60	0
16 June 1960	21	60	3
16 June 1960	21	60	3
16 June 1960	21	75	13
16 June 1960	21	75	9
16 June 1960	21	60	1
19 July 1960	14	75	0
19 July 1960	14	75	0
19 July 1960	14	75	4
19 July 1960	14	75	2
26 August 1960	11	60	2
26 August 1960	11	75	0
26 August 1960	11	60	0
26 August 1960	16	75	16
1 September 1960	10	60	0
1 September 1960	10	75	7
7 December 1961	19	120	21

[1] The location of each site is as follows:

	Elevation
Site #10—11 km north of Trail, Jackson Co.	850 m
Site #11—8 km west of Elkton, Douglas Co.	30 m
Site #14—8 km south of Eugene, Lane Co.	400 m
Site #16—3 km northwest of Drain, Douglas Co.	90 m
Site #19—10 km north of Oakland, Douglas Co.	200 m
Site #21—27 km northwest of Union Creek, Douglas Co.	850 m
Site #27—16 km northeast of Tiller, Douglas Co.	—
Site #55—1 km south of Selma, Josephine Co.	400 m

[2] Thirteen of these 56 larvae were small second instars congregated in the same general area and probably all from the egg complement of a single female.

December, most larvae were fairly well distributed vertically through the soil. (4) Of the 176 larvae represented in Figure 5, I collected 134, or 76% in a 50-cm stratum between 41 and 90 cm in depth.

The vertical distribution of *P. simi* larvae from eight collections at five sites (Fig. 6) reveals some interesting characteristics: (1) Frequency distributions A and B in March and May, respectively, show a large congregation of larvae in a 20-

Table 5. Larval densities of the six western Oregon species of *Pleocoma* in some coniferous forest and orchard soils.

| Species | No. larvae/m² | | Site |
	Minimum	Maximum	
P. dubitabilis	0	35	Douglas-fir forest
P. simi	0	56	Douglas-fir forest
P. carinata	0	15	Mixed conifer forest
P. oregonensis[1]	0	18	Beneath western yellow pine
P. oregonensis[1]	1	4	Beneath cherry tree
P. crinita[1]	5	84	Apple orchard
P. crinita	0	5	Mixed conifer forest
P. minor[1]	—	227	Apple orchard
P. minor	1	11	Mixed conifer forest

[1] Data from Ellertson and Ritcher (1959), recomputed from ft² to m².

cm stratum between 61 and 80 cm; in no other *P. simi* collection was there such a striking example of larval accumulation by depth. (2) Larvae presented in distribution C were taken in December at the same site as those in distributions A and B; there was, however, no accumulation of larvae at the lower depths in December when larvae were generally evenly distributed between 21 and 110 cm in the soil. (3) Though collected in 5 months and from four sites, larvae represented by distributions D–H were generally in the upper layers of soil, mostly above 60 cm in depth.

P. carinata larvae were collected at relatively shallow depths in the soil. Fifteen larvae collected on 21 May 1960 were generally less than 50 cm deep in the soil, and six collected on 28 March were shallower than 70 cm.

Most *P. dubitabilis* larvae collected during the 4 summer months (June to September) were generally fairly deep in the soil, usually below 40 cm (Fig. 5F–I). *P. simi* larvae collected at other sites during those 4 months were generally shallow in the soil, usually above 50 cm in depth, however (Fig. 6E–H).

Throughout this study, no *Pleocoma* larvae of any of the three species were found below 110 cm in depth. This is considerably more shallow than the maximum depth that larvae of other *Pleocoma* species and other genera of white grub have been observed. *P. minor* larvae have been found as deep as 149 cm (Ellertson and Ritcher, 1959) and *P. puncticollis* Rivers as deep as 240 cm (Linsley, 1938). Larvae of *P. linsleyi* Hovore have been taken at depths of between 60 and 240 cm (Hovore, 1971). Larvae, pupae, and adults of *P. conjungens lucia* Linsley have been collected from cells in rocky, clay soil at depths ranging from about 36 cm to several meters below the soil surface (Hovore, 1977). White grubs of the genus *Phyllophaga* have been found as deep as 190 cm in some Canadian soils (Hayes, 1929).

Environmental Factors Influencing Larval Distributions

On the basis of other Scarabaeid research, soil temperature, moisture, pH, and profile were considered most likely to directly or indirectly influence larval density in the soil, particularly vertical distribution, and to a lesser extent spatial distribution.
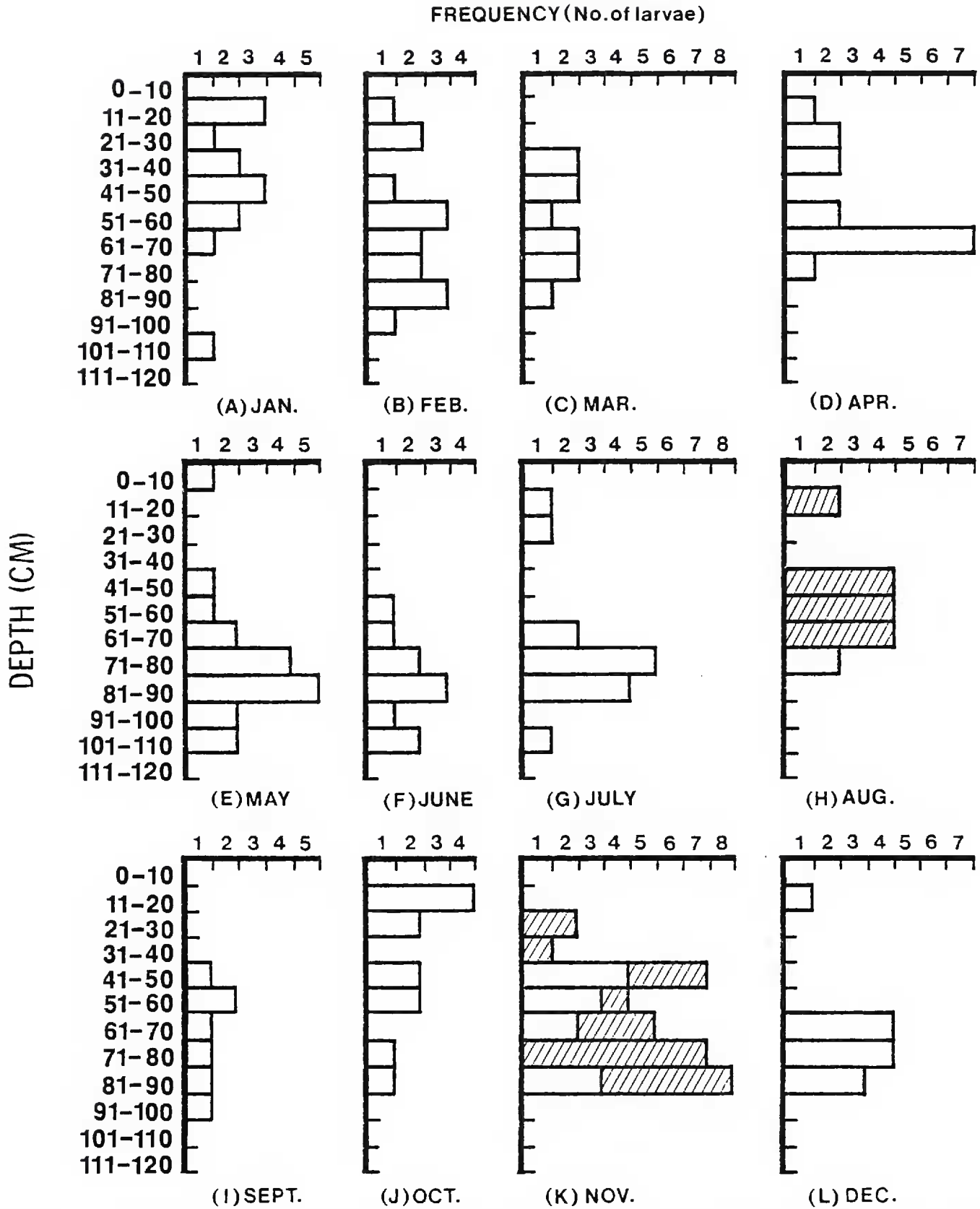
Figure 5. Vertical distribution of *Pleocoma dubitabilis* larvae in the soil at McDonald Forest in 1960 and 1961. Hatched blocks indicate larvae collected in 1960.

I collected soil samples at four depths—15, 45, 75, and 105 cm—in each sample hole to determine soil moisture content and soil pH.

Soil moisture was expressed in percentage of dry weight as outlined by Lyon and Buckman (1948). By their procedure, 100 grams of soil was mixed, weighed, air dried, and heated in an oven for 7 to 8 hours at 38 to 43°C, then cooled in a desiccator and weighed again.

Soil samples for pH determination were collected in 1-pint waxed cardboard containers. A 2-gram soil sample was suspended in 2 ml of distilled water in a 5-ml beaker. Micro-electrodes were immersed in the suspension and the pH read
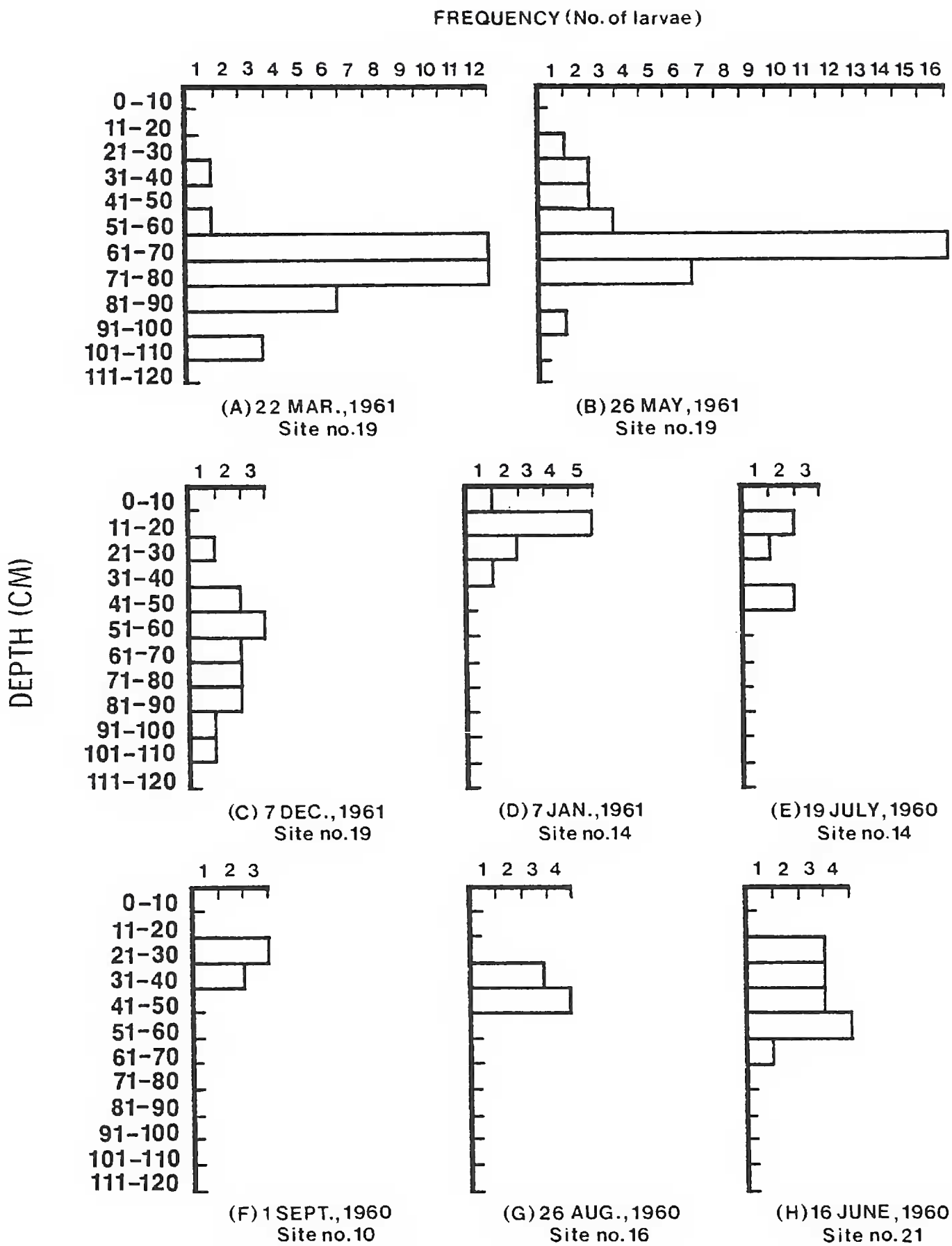
Figure 6. Vertical distribution of *Pleocoma simi* larvae in the soil at several forested sites in southwestern Oregon in 1960 and 1961. Locations of sites are described in footnote 1, Table 4.

on a Beckman Model N portable pH meter[3]. All measurements were first made using a buffer of pH 7; samples measuring 5.5 or below were rerun using a buffer of pH 4 for a more accurate reading.

[3] The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.
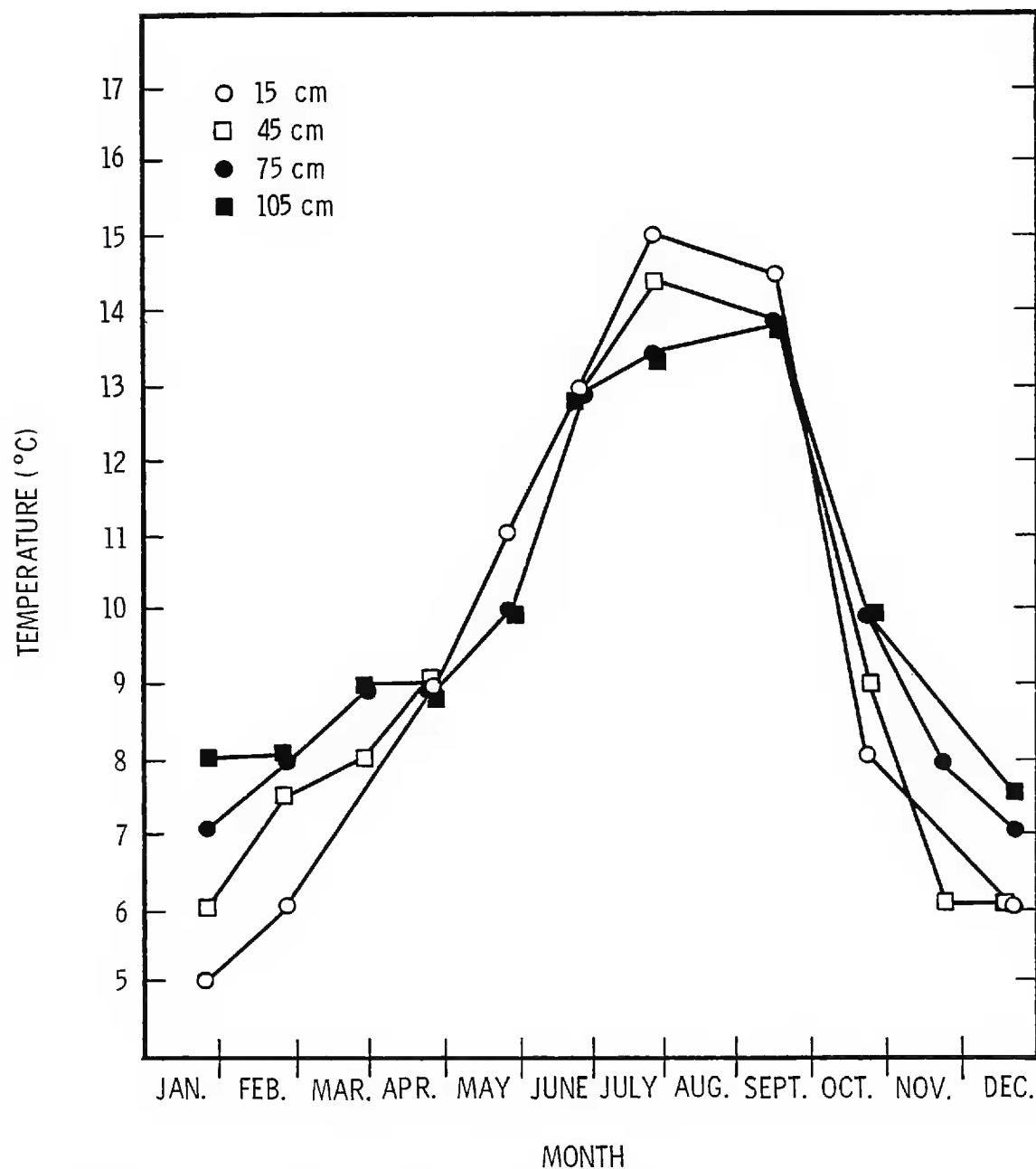
Figure 7.   Soil temperatures at four depths during 1961 at McDonald Forest study area, 8 km north of Corvallis.

At each of the four depths, I took soil temperatures by thrusting an ordinary immersion-type 110°C etched-stem thermometer at least 4 cm laterally into the soil and leaving it for at least 5 minutes before reading it.

The soil profile also was described for each sample hole.

Soil Temperature

At the McDonald Forest study area, where *P. dubitabilis* is found, soil temperatures at all depths were generally highest during the summer months and lowest during the late fall, winter, and early spring months. During the summer months, temperatures at the shallower depths were higher than those at lower depths, but during the winter months the reverse was true (Fig. 7). This transition in soil temperature was responsible for two temperature overturns during the year, when temperatures at all four depths were equal or nearly so. During the spring overturn in April, soil temperature at all four depths was 9°C while during the fall overturn in late September to early October 1961 temperatures at all four depths were 12 to 13°C.

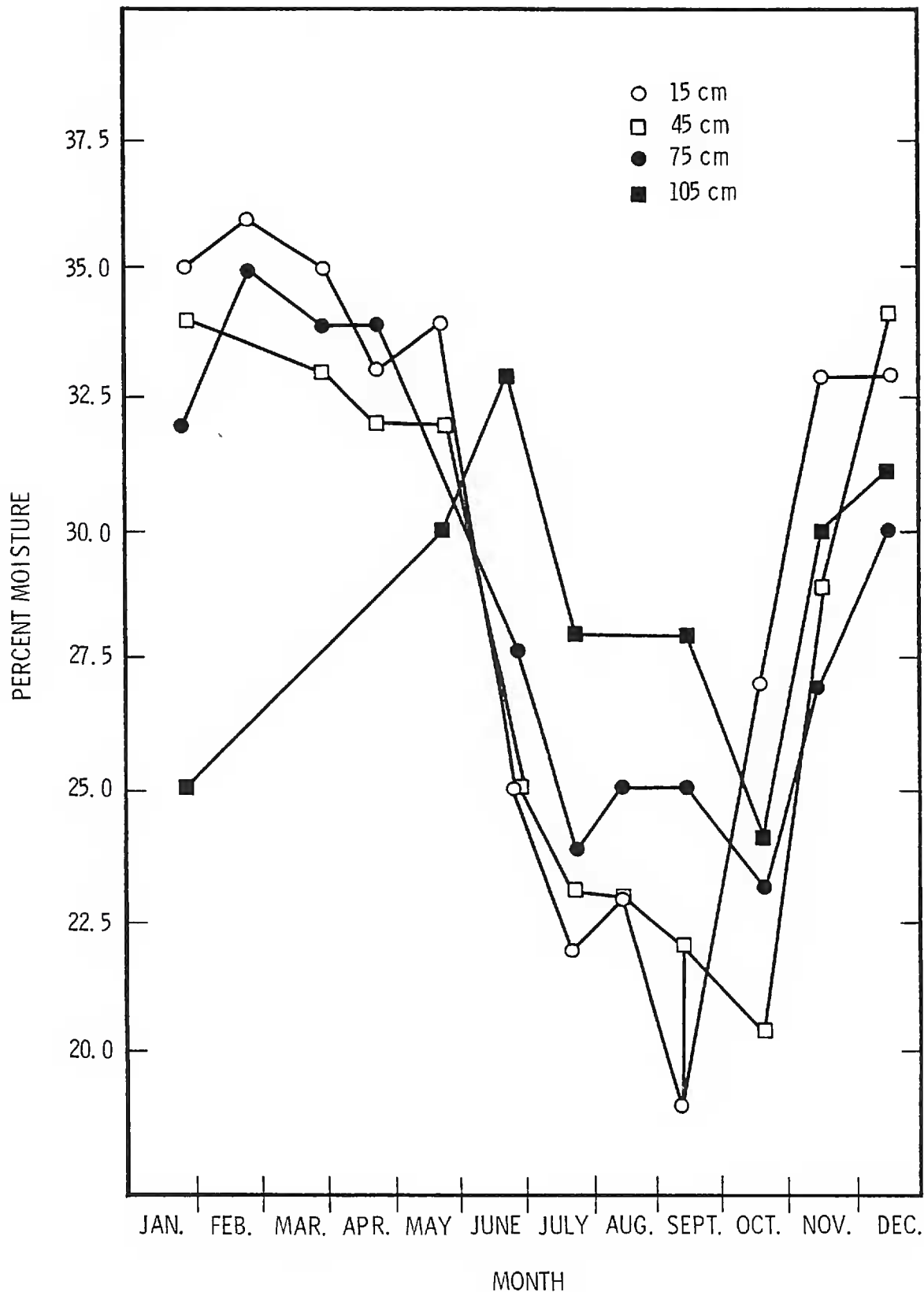The general absence of *P. dubitabilis* larvae above 40 cm during the 5 summer

Figure 8. Soil moistures at four depths during 1961 at the McDonald Forest study area, 8 km north of Corvallis.

months from May to September seems to be correlated with higher soil temperature at the 15-cm depth during this period. This is not a strong relationship, however, because temperatures at 45 and 75 cm during these 5 months were within 1 to 1.5°C of temperatures at 15 cm. Moreover, in May, July, and September, the difference in soil temperature between the 15- and 45-cm depths was only 0.5°C or less.

Pleocoma dubitabilis larvae did not appear to seek the soil stratum with the least temperature fluctuation. Had they done so, they should have been congregated at a depth of 105 cm or deeper, where soil temperatures throughout the year fluctuated the least (Fig. 7).

Soil temperatures taken with collections of *P. simi* and *P. carinata* larvae generally followed the same seasonal pattern as shown for the *P. dubitabilis* collections at the McDonald Forest study area (Fig. 7). Larvae of both *P. simi* and *P. carinata*, however, were generally shallower than 60 cm during summer months when temperatures were highest at the more shallow depths.

At least one site shows that no relationship appears to exist between soil temperature and vertical distribution of *P. simi* larvae (Fig. 6A–C). In May, when soil temperatures at 15 cm were higher than temperatures deeper in the soil, most larvae were congregated between 61 and 80 cm. In March, soil temperatures at 15 cm were cooler than those deeper in the soil, yet larvae were also congregated between 61 and 90 cm—even a more striking congregation than in May. During December, larvae were rather evenly distributed over a wide range in depths between 21 and 110 cm, and soil temperatures varied from 5.5°C at 15 cm to 8.0°C at 110 cm.

Soil Moisture

At the *P. dubitabilis* sites in McDonald Forest, percentage soil moisture was generally lower at all depths from June through October and higher from November through May. As with soil temperature, there was an overturn in soil moisture percentage twice a year, although the transposition in May to June and October to November is a bit indistinct (Fig. 8).

The generally drier soil at the 15- and 45-cm levels seems to be related to the absence of larvae at these levels from June through September (Fig. 5). In October, percentage soil moisture, though remaining low at 45 cm, increased at the 15-cm depth with the onset of fall rains, accompanied by the movement of some larvae to the more shallow depths (Fig. 5J). However, this apparent response to increased soil moisture is not supported by larval distributions in May and December (Fig. 5E, L). In those months, percentage soil moisture was highest at the 15- and 45-cm stratum, yet larvae were generally concentrated below 40 and 60 cm, respectively. October, November, and January to April moisture percentages at 15 and 45 cm were relatively high, yet larvae were reasonably well distributed in these strata. Other Scarabaeid larvae are known to move deeper into the soil as the upper layers dry out during the summer months (Shorey and Gyrisco, 1960; Rudolph, 1950).

Soil moisture percentages fluctuated least at the 105-cm level at the McDonald Forest study area in 1961 (Fig. 8). *Pleocoma dubitabilis* larvae, however, did not appear to search out the depth at which soil moisture was most stable or they would have congregated at 105 cm or deeper in the soil.

The relationship of *P. simi* and *P. carinata* larvae to percentage soil moisture is about the same as their respective relationship to soil temperatures. Soil moisture percentages taken with collections of larvae of these species are similar to the seasonal pattern shown for *P. dubitabilis* (Fig. 8). As was found with soil temperatures, larvae of *P. simi* and *P. carinata* generally burrowed at relatively shallow depths during that period of the year when the soil there was driest.

Although apparently only weakly related to vertical distribution of *Pleocoma* larvae, variations in percentage soil moisture could influence their spatial density. Infestations of other root-feeding Scarabaeid larvae are often light in poorly drained locations (Shorey et al., 1960; Nitto and Tachibana, 1955; Forbes, 1907; Smith

and Hadley, 1926). Excessively dry soil, however, can at times be detrimental to Scarab larvae (Smith and Hadley, 1926; Travis, 1939).

Soil pH

Soil pH did not appear to be a factor affecting the vertical distribution of *P. dubitabilis* larvae at McDonald Forest or *P. simi* or *P. carinata* at the various sites where they were collected. There was a slight increase in acidity with depth, averaging a pH of about 0.3 between 15 and 105 cm.

Though not apparently tied to vertical distribution of *Pleocoma* larvae, soil pH could influence their spatial density. A generally low pH seems to be correlated with higher larval population of the Japanese beetle (Polivka, 1960; Wessel and Polivka, 1952), *Phyllophaga* sp. (Hammond, 1949), and the European chafer (Shorey et al., 1960).

Soil Profile

Spatial distribution of *Pleocoma* larvae probably is not influenced by soil profile, but the vertical distribution of larvae apparently is influenced by the presence of a silicate clay horizon (hardpan or fragipan) at some sites. When a clay horizon was present, larvae were often congregated just above it, and when the horizon was absent there was usually no significant congregation of larvae by depth.

At the *P. dubitabilis* site at the McDonald Forest study area, no silicate clay horizon exists as attested by the vertical distribution of larvae collected there. Throughout the year there was no congregation of larvae at either shallow depths or deeper in the soil (Fig. 5); even in those months when I collected only a few larvae (i.e., September), they were rather well distributed vertically.

All collections of *P. simi* and *P. carinata* were made in coniferous forests in Lane, Douglas, and Jackson Counties, each lying in a major soil type characterized by horizons of silicate clay accumulation (Knox, 1962). The depth of the clay hardpan varied considerably between sites. At some sites it was relatively deep, 80 to 85 cm, and fairly regular, while at others it was as shallow as 15 cm and generally irregular and undulating.

The presence of a silicate clay hardpan at most sites where *P. simi* larvae were collected is reflected in the vertical distribution of larvae. At site #19, for example, a definite silicate clay hardpan existed at about 95 cm, and the horizon boundary was fairly regular. In all three collections at that site (Fig. 6A–C) the majority of the larvae were above 90 cm. The concentration of larvae immediately above that hardpan is particularly evident in the March and May collections (Fig. 6A, B). At other *P. simi* sites the hardpan was encountered at relatively shallow depths. Without exception, larvae collected at these sites were above the hardpan (Fig. 6D–H).

Clay hardpans and other soil characteristics are also known to affect the vertical movements of other Scarab larvae, especially *Phyllophaga* (Granovsky, 1958; Travis, 1939).

A silicate clay horizon may also affect maximum depth of oviposition, thus indirectly influencing vertical distribution of *Pleocoma* larvae, at least soon after hatching. On 8 July 1960, I collected a female *P. dubitabilis* and her 64 eggs at a forested site 3 miles north of Brownsville in Linn County. She was taken at 47

cm and her first eggs had been deposited at 58 cm. At about 60 cm there was a horizon of silicate clay accumulation.

DISCUSSION

The vertical distribution of *Pleocoma* larvae and, to a lesser extent, the spatial distribution probably are influenced by an interaction of factors. During the summer months most larvae probably avoid the upper layers of soil as temperatures there increase and the soil dries out. If no silicate clay layer is encountered, or if the hardpan is relatively deep, larvae are able to burrow as deep as necessary to find moisture and temperature conditions more suitable than near the surface. If a fairly shallow silicate clay layer is present, it obstructs the larvae in their movement downward while retreating from unsuitable conditions near the surface.

Because *Pleocoma* larvae are known to be capable of burrowing into very hard soil (Davis, 1934), including a hard clay layer, the silicate clay horizon may only indirectly restrict the downward movement of the larvae through the direct effect of the clay layer on tree roots. An obstructing layer such as a fragipan will cause a proliferation of Douglas-fir roots (and no doubt roots of other conifers) resulting in a greater density of rooting just above the fragipan (McMinn, 1963).

When the silicate clay layer is shallow, larvae probably tolerate suboptimum temperature and moisture conditions in the presence of abundant food (coniferous roots) immediately above the clay hardpan rather than burrow down into or below the rootless hardpan, even though temperature and moisture conditions there might be more suitable. This would account for finding many *P. simi* and *P. carinata* larvae at very shallow depths at sites where the silicate clay horizon was correspondingly shallow, even during summer months when most larvae in soils without shallow hardpans are deeper in the soil. In orchard soils, Ellertson and Ritcher (1959) found the character of the subsoil affected penetration of orchard tree roots and the vertical distribution of *P. crinita* and *P. minor*.

At the McDonald Forest study area, many prepupal *P. dubitabilis* larvae were found at depths less than 30 cm during the summer months when all other larvae at that area were deeper in the soil. This indicates that the intrinsic behavioral trait to pupate at shallow depths outweighed the effect of warmer and drier soil— apparently unfavorable to most larvae. In these cases then, the physiological or developmental state of the larvae is yet another factor influencing the vertical distribution of *Pleocoma* larvae in the soil.

With other Scarabaeids a complex interaction of factors is responsible for the vertical movements of larvae (Fidler, 1936; Smith and Hadley, 1926; Nakashima, 1952; McCulloch and Hayes, 1923; Granovsky, 1956).

Different types of soil probably influence the spatial distribution and density of *P. dubitabilis, P. simi,* and *P. carinata,* as they apparently do larvae of other species of *Pleocoma.* The larvae of *P. behrensii* LeConte are found in soils that are "... usually of a rich loamy or clayey nature, intermixed with humus ..." (Rivers, 1890). And in collecting *P. fimbriata* LeConte, Hopping (1920) always found females "... in the red soil." At the type locality of three new sympatric *Pleocoma—P. marquai* Hovore, *P. rubiginosa* Hovore, and *P. hirticollis reflexa* Hovore (all described by Hovore, 1972)—larvae showed no apparent preference for a particular soil type as the soils vary from hardpacked, decomposing granite to a loose clay loam. Stein (1963) summarized the available information and,

though fragmentary, it clearly demonstrates that species of *Pleocoma* inhabit a variety of soils. With other Scarab genera, lighter soils are more heavily infested with *Phyllophaga* than heavier ones (Seamans, 1956), and highly impervious soils are detrimental to Japanese beetle larvae (Smith and Hadley, 1926).

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